

Populations under frequency-dependent selection and genetic drift: a genealogical approach

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Abstract

Evolutionary models for populations of constant size are frequently studied using the Moran model, the Wright–Fisher model, or their diffusion limits. When evolution is neutral, a random genealogy given through Kingman’s coalescent is used in order to understand basic properties of such models. Here, we address the use of a genealogical perspective for models with weak frequency-dependent selection, i.e. $Ns =: \alpha$ is small, where s is the fitness advantage of a fit individual and N is the population size. When computing fixation probabilities, this leads either to the approach proposed by Rousset (2003), who argues how to use Kingman’s coalescent in order to study weak selection, or to extensions of the ancestral selection graph of Neuhauser and Krone (1997) and Neuhauser (1999). As an application of this genealogical approach, we re-derive the one-third rule of evolutionary game theory (Nowak et al., 2004). In addition, we provide the approximate distribution of the genealogical distance of two randomly sampled individuals under linear frequency-dependence.

1 Introduction

Evolutionary game theory has long been studied using replicator equations and deterministic systems by using an infinite population limit (Taylor and Jonker, 1978; Maynard-Smith, 1982; Nowak, 2006). Recently, the amount of research dealing with repeated games in finite populations increases. In the simplest case, a population of N players (each carrying one out of a possible set of strategies) repeatedly chooses an opponent at random and plays a game with payoff matrix M . In addition, players can produce offspring and the fitness of an individual with strategy A is determined by the average payoff the player obtains in the evolutionary game. Since the average payoff depends on the frequencies of the strategies in the population, the fitness is frequency-dependent, and the frequency path is e.g. given by a Moran model or a Wright–Fisher model with frequency-dependent selection.

When studying models for populations of individuals carrying different types (or adopting different strategies), several questions are most important (see e.g. Ewens, 2004). What is the probability of fixation of a type (in absence of mutation), or what is the random distribution of types in mutation-selection balance? If fixation occurs, what is the distribution of the fixation time? When taking a sample from the population, what is its genealogical structure? In addition, extensions to structured populations or to the multi-type case are considered. For the questions on fixation probabilities and times, the theory of birth-death processes and (one-dimensional) diffusions is frequently used (Karlin and Taylor, 1981). Here, explicit formulas are available for such quantities, but these can hardly be extended to multi-dimensional cases. Another approach

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is the use of the genealogical structure by coalescent processes (Kingman, 1982; Berestycki, 2009). The advantage is that it is extensible to populations in structured or multi-type populations. In addition, questions on the genealogical structure can be asked. As an example from evolutionary game theory, Gokhale and Traulsen (2011) study the frequency path of many-player many-strategy games using such a genealogical approach.

The current paper was motivated by the *one-third rule* of evolutionary game theory (Nowak et al., 2004). It states that in finite populations of players with two strategies A and B , strategy A is favored in the sense that the fixation probability of type A in a B -population is higher than under neutrality if and only if type A is favored in the infinite population limit at frequency $1/3$. Since the one-third rule was found in a Moran model, it has as well been proven to hold in a Wright–Fisher model (Traulsen et al., 2006; Imhof and Nowak, 2006) and in general exchangeable models (Lessard and Ladret, 2007). An intuitive explanation was given in Ohtsuki et al. (2007), who argue that an individual interacts on average with B -players twice as often as with A -players, which implies the one-third rule. Wu et al. (2010) discuss violations of the one-third rule for non-linear frequency dependence.

The goal of the present paper is to use a genealogical approach in the study of fixation probabilities. Only Ladret and Lessard (2007), who use a method developed by Rousset (2003), already take this route; see also Rousset (2004), p. 92f. We complement their approach by using the Ancestral Selection Graph (ASG), first introduced in the frequency-independent case by Neuhauser and Krone (1997) and Krone and Neuhauser (1997). This graph extends the coalescent to the selective case and has been further extended to a simple frequency-dependent case in Neuhauser (1999). In addition, we study genealogical distances in models from evolutionary game theory, i.e. frequency-dependent selection.

The paper is organized as follows: After stating the models (and their diffusion limits), we re-formulate the one-third rule and our results on genealogical distances. Then, we provide two proofs of the one-third rule. Finally our genealogical result is proved.

2 Models

We are studying the solution $\mathcal{X} = (X_t)_{t \geq 0}$ of the stochastic differential equation

$$dX = ((1 - X)\theta_A - X\theta_B)dt + \alpha X(1 - X)(\beta - \gamma X)dt + \sqrt{X(1 - X)}dW \quad (2.1)$$

for $\alpha, \theta_A, \theta_B \geq 0, \beta, \gamma \in \mathbb{R}$. Here, α is called the *scaled selection coefficient*, and θ_A and θ_B the *scaled mutation rates*, and \mathcal{X} gives the frequency path of type (or strategy) A in a population of constant size. For this diffusion, we define in the case $\theta_A = \theta_B = 0$

$$T_1 := \inf\{t \geq 0 : X_t = 1\}$$

and note that $T_1 < \infty$ if and only if type- A eventually fixes in the population. In our analysis, the version of (2.1) without mutation and without fluctuations,

$$dx = \alpha x(1 - x)(\beta - \gamma x)dt \quad (2.2)$$

will also play a role.

2.1 A finite Moran model

We are turning to the frequency path of strategy (or type) A in a time-continuous Moran model of size N , which converges to \mathcal{X} as $N \rightarrow \infty$. We distinguish four cases, corresponding to the signs of β and γ . Setting $x_* = \beta/\gamma$ (which is an equilibrium point in (2.2)), the four cases are:

- (i) $\beta > 0$ and $\gamma > 0$, which leads to a stable fixed point in x_* for (2.2) (if $x_* \in (0, 1)$),

- (ii) $\beta < 0$ and $\gamma < 0$, which leads to an unstable fixed point in x_* for (2.2) (if $x_* \in (0, 1)$),
- (iii) $\beta > 0$ and $\gamma < 0$, which leads $x = 1$ as the only stable fixed point in (2.2),
- (iv) $\beta < 0$ and $\gamma > 0$, which leads $x = 0$ as the only stable fixed point in (2.2).

In case (ii) and (iv), strategy A cannot invade a population consisting only of strategy B individuals in (2.2) and vice versa.

The time-continuous Moran model is a Markov process with state space $\{A, B\}^N$ (indicating the types of N individuals) and the following transition rules:

1. Every pair of individuals i and j resamples at rate 1. Upon a resampling event, the offspring of i (or j) replaces j (or i) with probability $\frac{1}{2}$.
- 2A. In cases (i) and (iii), i.e. when $\beta > 0$, the offspring of any A -individual replaces a randomly chosen individual at rate $\alpha\beta$.
- 2B. In cases (ii) and (iv), i.e. when $\beta < 0$, the offspring of any B -individual replaces a randomly chosen individual at rate $-\alpha\beta = \alpha|\beta|$.
- 3A. In cases (i) and (iv), i.e. when $\gamma > 0$, every B -individual picks a randomly chosen individual at rate $\alpha\gamma$. If it is an A -individual, an offspring of the B -individual replaces another, randomly chosen individual.
- 3B. In cases (ii) and (iii), i.e. when $\gamma < 0$, every A -individual picks a randomly chosen individual at rate $-\alpha\gamma = \alpha|\gamma|$. If it is another A -individual, an offspring of the first A -individual replaces another, randomly chosen individual.
4. Every individual is hit by a mutation event at rate $\bar{\theta} := \theta_A + \theta_B$. With probability $\theta_A/\bar{\theta}$, the individual turns into type A , and with probability $\theta_B/\bar{\theta}$, it turns to B , independent of the type of the parent.

In the graphical construction of the Moran model, the transitions 1.–3. are given by arrows denoted T1-T3, respectively. The T3-arrows are in fact double-arrows since the type of one individual has to be checked (along the line which we will call the checking line; see also Neuhauser (1999)) while the second arrow leads to reproduction (which will be called the imitating line). See Figures 1 and 2 for illustrations of the transitions 1., 2. and 3. By now, it is a classical result that the frequency path of the Moran model converges weakly (with respect to the topology of uniform convergence on compact sets) to solutions of (2.1); see e.g. Ethier and Kurtz (1993).

2.2 Connection with evolutionary games

Consider a game with payoff matrix

	A	B
A	a	b
B	c	d

There are N players, each one adopting either strategy (or type) A or B . If the frequencies of type A and type B are X_A and X_B , respectively, the fitnesses are dependent on the payoff matrix and are given by

$$\begin{aligned} f_A &:= \frac{1}{2} + s(aX_A + bX_B) = \frac{1}{2} + s(b + (a - b)X_A), \\ f_B &:= \frac{1}{2} + s(cX_A + dX_B) = \frac{1}{2} + s(d + (c - d)X_A). \end{aligned} \tag{2.3}$$

Note that $aX_A + bX_B$ is the average payoff of a type- A individual when playing against a random player from the population.

Here, the offspring of every individual of type A replaces a randomly chosen individual at rate f_A . Accordingly, a type- B offspring replaces a randomly chosen individual at rate f_B (given that

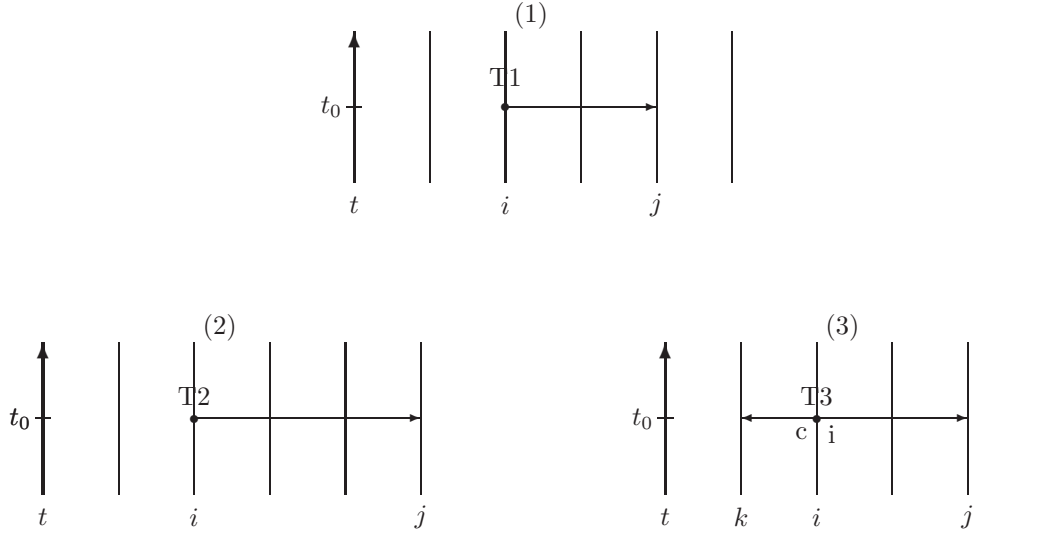


Figure 1: Three different kinds of events occur in the Moran model which has limit (2.1). (1) For every (ordered) pair of individuals i and j , a T1-arrow occurs at rate $\frac{1}{2}$. Here, the offspring of i replaces individual j (independent of the types of i and j). (2) T2-arrows are the first of two selective arrows. In cases (i) and (iii) (cases (ii) and (iv)), they occur at rate $\alpha\beta$ (at rate $-\alpha\beta$). Upon such an event, the offspring of individual i replaces j , given that i has type A (type B). (3) T3-(double-)arrows, occur in case (i) and (iv) (cases (ii) and (iii)) at rate $\alpha\gamma$ (at rate $-\alpha\gamma$). Here, the imitating arrow is created from i to j , as well as the checking arrow from i to k . Given i has type B (type A) the checked individual k has type A (in both cases), individual j is replaced by an offspring of individual i .

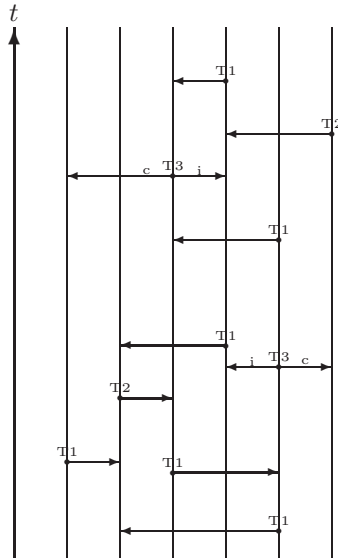


Figure 2: The graphical representation of the Moran model (without mutation). Here, every pair of individuals is connected by a T1-arrow at rate 1, every individual is the origin of a T2-arrow at rate $\alpha|\beta|$, and every individual is origin of a T3-double-arrow to one checking and one imitating line at rate $\alpha|\gamma|$. Types/strategies are inherited along the arrows according to the rules 1.–3.

s is small enough such that the rates are non-negative). The frequency path of type- A , follows in the infinite-population limit, $N \rightarrow \infty$,

$$dx = sx(1-x)(b + (a-b)x - d - (c-d)x)dt = sx(1-x)(\beta - \gamma x)dt$$

with

$$\beta := b - d, \quad \gamma := b - d + c - a. \quad (2.4)$$

Moreover, when $N \rightarrow \infty$, $s \rightarrow 0$ such that $Ns \rightarrow \alpha$, and time is rescaled by a factor of N , the frequency path of type- A follows the SDE as given in (2.1). Since the Moran model from Section 2.1 has the same diffusion limit, we use its graphical representation in order to obtain insights into the evolutionary game just described.

3 Results

Starting by re-formulating the *one-third rule* in Section 3.1, we give our result on the distribution of genealogical distances in the Moran model from Section 2.1 in Section 3.2.

3.1 The one-third rule

We are now ready to formulate the one-third rule. For $\theta_A = \theta_B = 0$, we define

$$p_{\text{fix}}(\varepsilon, \alpha) := \mathbf{P}(T_1 < \infty | X_0 = \varepsilon),$$

which is the fixation probability of type A if it starts in frequency ε and selection intensity is α . Note that $p_{\text{fix}}(\varepsilon, 0) = \varepsilon$, i.e. the chance that strategy A fixes equals its starting frequency, if evolution is neutral.

Theorem 1 (One-third rule, Nowak et al. (2004)). *Let $\mathcal{X} = (X_t)_{t \geq 0}$ be the solution of (2.1) with $\theta_A = \theta_B = 0$. Then,*

$$\lim_{\alpha \rightarrow 0} \frac{1}{\alpha \varepsilon} (p_{\text{fix}}(\varepsilon, \alpha) - \varepsilon) \xrightarrow{\varepsilon \rightarrow 0} \beta - \gamma \frac{1}{3}.$$

In particular, $p_{\text{fix}}(\varepsilon, \alpha) > p_{\text{fix}}(\varepsilon, 0)$ for α, ε small enough, if and only if

$$\beta - \gamma \frac{1}{3} > 0,$$

i.e. the fitness of type A is above average at frequency $x = \frac{1}{3}$.

In Section 5, we will provide two different proofs of this result. The first proof goes back to Ladret and Lessard (2007), the second one uses the ancestral selection graph which we introduce in Section 4.

3.2 Genealogical distances

In order to precisely formulate our results on genealogical distances, we are considering the Moran model from Section 2.1 including mutation, i.e. $\theta_A, \theta_B > 0$. Assume that the Moran model (which evolves according to the rules 1.–4.) has run for an infinite amount of time. Then, every pair of individuals has a most recent common ancestor which can be read off from the graphical representation; see Figure 2.

Here, we denote by $\mathbf{P}_{N,\alpha}$ the distribution of the Moran model with population size N and selection coefficient α in equilibrium, and by $\mathbf{E}_{N,\alpha}$ the corresponding expectation. Note that the Moran model is finite and hence, the equilibrium exists and is unique. Moreover, we denote by R_{12}

the genealogical distance of two randomly sampled individuals from the equilibrium population. In the case $\alpha = 0$, recall that the distance of two randomly sampled individuals is exponentially distributed, and hence, $\mathbf{E}_{N,\alpha=0}[e^{-\lambda R_{12}}] \xrightarrow{N \rightarrow \infty} 1/(1 + \lambda)$. The following result generalizes this fact to small α , i.e. weak selection.

Theorem 2 (Genealogical distances under weak frequency-dependent selection).

Let $\mathbf{E}_{N,\alpha}$ and R_{12} be as above. Then, with $\bar{\theta} = \theta_A + \theta_B$,

$$\lim_{N \rightarrow \infty} \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] = \frac{1}{1 + \lambda} - \alpha\gamma \frac{\theta_A \theta_B}{\bar{\theta}} \frac{(2 + \bar{\theta} + \lambda)\lambda}{(6 + \bar{\theta} + \lambda)(3 + \bar{\theta} + \lambda)(1 + \bar{\theta} + \lambda)(1 + \bar{\theta})(1 + \lambda)^2} + \mathcal{O}(\alpha^2).$$

In particular,

$$\lim_{N \rightarrow \infty} \mathbf{E}_{N,\alpha}[R_{12}] = 1 + \alpha\gamma \frac{\theta_A \theta_B}{\bar{\theta}} \frac{2 + \bar{\theta}}{(6 + \bar{\theta})(3 + \bar{\theta})(1 + \bar{\theta})^2} + \mathcal{O}(\alpha^2)$$

Remark 3.1. 1. Note that – up to first order in α – the change in the genealogical distance only depends on γ but not on β . This is not surprising since it has been shown that in the case of frequency-independent selection, $\beta = 1, \gamma = 0$, the change in the genealogical distance is of order α^2 ; see Theorem 4.26 in Krone and Neuhauser (1997). However, this leads to an interesting effect: assume that $\beta > \gamma > 0$. Then, type A is selectively advantageous at any time during the evolution of the population. So, one might guess that type- A individuals have a higher chance to get offspring and genealogical distances are shorter than under neutrality. However, as the result shows, up to first order in α , genealogical distances are larger than under neutrality. The reason is that for $\gamma > 0$, selection is strongest by frequent interactions between A and B individuals, and such interactions require a high heterozygosity, which in turn requires larger genealogical distance.

2. In our proof, we implicitly take advantage of the recently developed theory of tree-valued stochastic processes from Greven et al. (2012) and Depperschmidt et al. (2012). The idea is to describe the evolution of the genealogical distance of two randomly sampled points. If no events hit the two lines, the distance grows at constant speed. If a T1-arrow falls in between the two sampled individuals, their distance is reset to 0. Finally, with high probability, the two sampled lines are hit by T2- or T3-arrows only if the arrows originate from one of the $N - 2$ other individuals. Once the evolution of the distance of two randomly sampled lines is given, we only have to find a(n approximate) fixed point in order to show Theorem 2. The details are given in Section 6.

4 The ASG for linear frequency-dependent selection

The ancestral selection graph (ASG) was introduced by Neuhauser and Krone (1997) and Krone and Neuhauser (1997) in order to study genealogies in the case of frequency-independent selection. Later, it was extended in Neuhauser (1999) to a model of minority-advantage, a special form of frequency-dependence in an infinite alleles setting.

Here, we introduce the ASG in order to give a proof of Theorem 1. For its construction, consider again Figure 2. If a sample of individuals is drawn at the top of the figure, one can read off all events which finally determine their types. Because there are three different kinds of arrows, the history of the sample as well comes with three different events. First, T1-arrows between lines in the sample lead to coalescence events, because common ancestors are found along such events. Second, T2-arrows mostly origin from lines outside the sample. Since they as well are determinants of the types in the sample, such events lead to branching events into a continuing and an incoming branch. Third, T3-arrows lead to splits of a line into the continuing, the checking and the imitating line.

This informal description turns into the following stochastic process: Starting with n lines, the following transitions occur:

1. Every pair of lines coalesces at rate 1.
2. Every single line splits in two (called the continuing and incoming line) at rate $\alpha|\beta|$.
3. Every single line splits in three (called the continuing, checking and imitating line) at rate $\alpha|\gamma|$.

Consider again the graphical representation of the Moran model from Figure 2. Here, starting with n lines at the top of the figure, it might be that the last event which hits one of the n lines is a T2- or T3-arrow, which originates from one of the n lines. However, since N is assumed to be large, and the $N \rightarrow \infty$ limit gives (2.1), this case can be ignored in the limit.

Once this graph is run for time t (i.e. from time t down to time 0), and the starting frequency of type A (at time 0) of the forward process is given, we can determine the configuration of the n lines. First, assign randomly each of the lines of the ASG at time 0 with A according to the starting frequency. Then, go through the ASG from time 0 up to time t . The types are inherited along every T1-arrow. Moreover, we have to distinguish the inheritance rules in the four cases, (i)–(iv).

- 2A In cases (i) and (iii), i.e. when $\beta > 0$, the type of the incoming branch is inherited if it has type A . Otherwise the type of the continuing branch is inherited.
- 2B In cases (ii) and (iv), i.e. when $\beta < 0$, the type of the incoming branch is inherited if it has type B . Otherwise the type of the continuing branch is inherited.
- 3A In cases (i) and (iv), i.e. when $\gamma > 0$, the type of the imitating branch is inherited if it has type B and the checking branch has type A . Otherwise the type of the continuing branch is inherited.
- 3B In cases (ii) and (iii), i.e. when $\gamma < 0$, the type of the imitating branch is inherited if it has type A and the checking branch has type A . Otherwise the type of the continuing branch is inherited.

It is important to understand that these rules are reminiscent of the corresponding transitions in the Moran model. As an example, consider Figure 3(D). (Here, the ASG is given starting with a single line at the top, $n = 1$.) In case (i) and (iv), the type of the line at the top is A only if both lines at the bottom have type A . If the first line is B , the continuing branch of the T3-event is followed which carries type B . If the first line is A and the second line is B , rule 3A says that the type of the imitating branch is inherited, hence the line at the top has type B . In case (ii) and (iii), the line at the top is A if and only if the first line at the bottom is type A . In this case, the imitating line can only be used if it has type A as well, leading to type A at the top. If the first line carries B , the continuing line is used at the T3-event, leading to type B at the top. In Table 1, we assume that the frequency of type A at time 0 is $\varepsilon \ll 1$, and we give all possibilities which lead to fixation of type A , which require at most one type- A individual in the past, and their respective probabilities up to order ε .

5 Two proofs of Theorem 1

5.1 A proof based on Rousset (2003) and Ladret and Lessard (2007)

Although the proof of Ladret and Lessard (2007), which is based on ideas from Rousset (2003) is carried out in a time-discrete model, the same argument works for the SDE (2.1). Again, we write $\mathbf{E}_{\varepsilon, \alpha}[\cdot]$ for expectations with $X_0 = \varepsilon$ and fitness coefficient α . First, (2.1) is continuous in the parameter α , such that $\mathbf{E}_{\varepsilon, \alpha}[f(X_t)] = \mathbf{E}_{\varepsilon, 0}[f(X_t)](1 + \mathcal{O}(\alpha))$ for $f \in \mathcal{C}_b^2(\mathbb{R})$. Moreover, by the

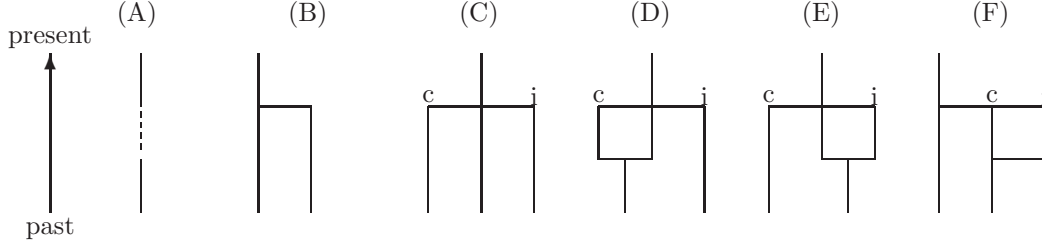


Figure 3: All different possible events/genealogies in the ancestral selection graph (ASG) connected to (2.1). Time in the ASG is running from top to bottom, i.e. from the present to the past. (A) In this case, when picking a single line in the present, its type only depends on the type of its ancestor, which is the single line at the bottom. (B) A T2-arrow leads to a split of a single line into a (straight) continuing line and an incoming line. In case (i) (case (ii)), if the incoming line has type A (type B), the type at the top is type A (type B) as well. If the incoming line has type B (type A), the type at the top equals the type of the continuing line. Here, the type of the line in the present depends on the types of both lines at the bottom. (C) A T3-arrow leads to a split of a single line in the checking (c), imitating (i) and continuing line. Here, in case (i) (case (ii)), if the checking line is type A (in both cases), and the imitating branch is type B (type A), the type at the top is type B (type A) as well. In all other cases, the type at the top equals the type of the continuing line. (D), (E), (F) In addition to a T3-branching event, coalescence of two lines might happen, leading to two lines present in the ASG at the bottom of the time window.

Genealogy $\mathcal{G} = g$						
Case (i): in which cases does A fix?						
Case (i): $\mathbf{P}[A \text{ fixes} \mathcal{G} = g, X_0 = \varepsilon]$	ε	2ε	ε	0	ε	ε
Case (ii): in which cases does A fix?						
Case (ii): $\mathbf{P}[A \text{ fixes} \mathcal{G} = g, X_0 = \varepsilon]$	ε	0	ε	ε	ε	2ε
Case (iii): in which cases does A fix?						
Case (iii): $\mathbf{P}[A \text{ fixes} \mathcal{G} = g, X_0 = \varepsilon]$	ε	2ε	ε	ε	ε	2ε
Case (iv): in which cases does A fix?						
Case (iv): $\mathbf{P}[A \text{ fixes} \mathcal{G} = g, X_0 = \varepsilon]$	ε	0	ε	0	ε	ε

Table 1: All possible genealogies close to time 0 in the ASG for small selection strength α and a small starting frequency $X_0 = \varepsilon \ll 1$. In the second (fourth, sixth, eighth) line we indicate which of the lines at the bottom has to be type A such that type A fixes in case (i) (case (ii), case (iii), case (iv)). In the third (fifth, seventh, ninth) line we give the corresponding probabilities (with error terms of order ε^2).

duality of the Wright–Fisher diffusion, i.e. (2.1) with $\alpha = 0$, to Kingman’s coalescent,

$$\begin{aligned}\mathbf{E}_{\varepsilon,0}[X_t(1-X_t)] &= e^{-t}\varepsilon(1-\varepsilon) = e^{-t}(\varepsilon + \mathcal{O}(\varepsilon^2)), \\ \mathbf{E}_{\varepsilon,0}[X_t^2(1-X_t)] &= e^{-3t}\varepsilon^2(1-\varepsilon) + \int_0^t 3e^{-3s}e^{-(t-s)}\frac{1}{3}\varepsilon(1-\varepsilon)ds \\ &= \frac{1}{2}e^{-t}(1-e^{-2t})(\varepsilon + \mathcal{O}(\varepsilon^2))\end{aligned}$$

as $\varepsilon \rightarrow 0$. Here, the first equation arises since $2X_t(1-X_t)$ is the probability to obtain two different types when picking from the population. This event requires that the two sampled individuals do not share an ancestor between times 0 and t . Moreover, both ancestors have to have different types. For the second equality, when sampling three individuals, two of which are type A , there are two possibilities. Either no coalescence of the three sampled lines occurred between times 0 and t , or two of three lines coalesced and have a type A -ancestor. Combining these results,

$$\begin{aligned}\mathbf{P}_{\varepsilon,\alpha}(A \text{ fixes}) &= \mathbf{E}_{\varepsilon,\alpha}[X_\infty] = \varepsilon + \int_0^\infty \frac{d}{dt}\mathbf{E}_{\varepsilon,\alpha}[X_t]dt \\ &= \varepsilon + \alpha \int_0^\infty \mathbf{E}_{\varepsilon,0}[X_t(1-X_t)(\beta - \gamma X_t)](1 + \mathcal{O}(\alpha))dt \\ &= \varepsilon + \alpha \int_0^\infty (\beta e^{-t}(\varepsilon + \mathcal{O}(\varepsilon^2)) - \frac{1}{2}\gamma e^{-t}(1-e^{-2t})(\varepsilon + \mathcal{O}(\varepsilon^2)))(1 + \mathcal{O}(\alpha))dt \\ &= \varepsilon \left(1 + \alpha \left(\beta - \gamma \frac{1}{3}\right)\right) + \mathcal{O}(\alpha^2, \varepsilon^2),\end{aligned}$$

which finishes the first proof.

5.2 A proof based on the ASG

Let us prove Theorem 1 by using the ASG. Here, type A eventually fixes if and only if the common ancestor of all individuals carries type A . Therefore, we have to study the ASG which has run for an infinite amount of time (i.e. from time infinity back to time 0). Since α is assumed to be small, we can assume that the ASG has only a single line at time 0 with high probability. However, with probability of order α , the ASG has split close to time 0 but the resulting lines have not fully coalesced yet. Since α is small, we can assume that the last split event happened when the ASG only had a single line.

In Figure 3, we list all possible ASGs near time 0 which we have to consider. Start with case (B), which is a split in two lines. We abbreviate this genealogy by $\begin{array}{c} | \\ \hline \end{array}$. Noting that such split events occur at rate $\alpha|\beta|$, and coalescence of the resulting two lines happens at rate 1, the probability for this case is (by competing exponential clocks)

$$\mathbf{P}\left(\begin{array}{c} | \\ \hline \end{array}\right) = \frac{\alpha|\beta|}{1 + \alpha|\beta|} + \mathcal{O}(\alpha^2) = \alpha|\beta| + \mathcal{O}(\alpha^2). \quad (5.1)$$

Similarly, consider the case when the last split occurs into three lines, which do not coalesce up to time 0 (case $\begin{array}{c} | \\ \hline \hline \end{array}$). Since coalescence of any pair happens at rate 3, we obtain

$$\mathbf{P}\left(\begin{array}{c} | \\ \hline \hline \end{array}\right) = \frac{\alpha|\gamma|}{3 + \alpha|\gamma|} + \mathcal{O}(\alpha^2) = \frac{\alpha|\gamma|}{3} + \mathcal{O}(\alpha^2). \quad (5.2)$$

Finally, the last split can lead to three lines and two of them coalesce up to time 0. Since all three

possible genealogies (denoted $\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}$, $\begin{array}{c} | \\ \diagup \\ | \end{array}$ and $\begin{array}{c} | \\ \diagdown \\ | \end{array}$) have equal probability, we obtain

$$\mathbf{P}\left(\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}\right) = \mathbf{P}\left(\begin{array}{c} | \\ \diagup \\ | \end{array}\right) = \mathbf{P}\left(\begin{array}{c} | \\ \diagdown \\ | \end{array}\right) = \frac{1}{3} \frac{\alpha|\gamma|}{1+\alpha|\gamma|} + \mathcal{O}(\alpha^2) = \frac{\alpha|\gamma|}{3} + \mathcal{O}(\alpha^2). \quad (5.3)$$

Last, we have for the remaining case $\begin{array}{c} | \\ | \\ | \end{array}$

$$\begin{aligned} \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) &= 1 - \mathbf{P}\left(\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}\right) - \mathbf{P}\left(\begin{array}{c} | \\ \diagup \\ | \end{array}\right) - \mathbf{P}\left(\begin{array}{c} | \\ \diagdown \\ | \end{array}\right) + \mathcal{O}(\alpha^2) \\ &= 1 - \alpha\left(|\beta| + \frac{4}{3}|\gamma|\right) + \mathcal{O}(\alpha^2). \end{aligned} \quad (5.4)$$

Using Table 1 for the probabilities of fixation conditioned on the genealogy, we can now collect all terms in the four cases. We obtain

$$\begin{aligned} \text{Case (i): } p_{\text{fix}}(\varepsilon, \alpha) &= \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + 2\varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagdown \\ | \end{array}\right) \\ &\quad + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + \mathcal{O}(\alpha^2, \varepsilon^2) \end{aligned}$$

$$\begin{aligned} \text{Case (ii): } p_{\text{fix}}(\varepsilon, \alpha) &= \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagdown \\ | \end{array}\right) \\ &\quad + 2\varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + \mathcal{O}(\alpha^2, \varepsilon^2) \end{aligned}$$

$$\begin{aligned} \text{Case (iii): } p_{\text{fix}}(\varepsilon, \alpha) &= \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + 2\varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagdown \\ | \end{array}\right) \\ &\quad + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + 2\varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + \mathcal{O}(\alpha^2, \varepsilon^2) \end{aligned}$$

$$\text{Case (iv): } p_{\text{fix}}(\varepsilon, \alpha) = \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ | \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \diagdown \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagup \\ | \end{array}\right) + \varepsilon \cdot \mathbf{P}\left(\begin{array}{c} | \\ \diagdown \\ | \end{array}\right) + \mathcal{O}(\alpha^2, \varepsilon^2)$$

Plugging in the probabilities from (5.1), (5.2), (5.3) and (5.4), we obtain in all cases

$$p_{\text{fix}}(\varepsilon, \alpha) = \varepsilon \left(1 + \alpha \left(\beta - \gamma \frac{1}{3}\right)\right) + \mathcal{O}(\alpha^2, \varepsilon^2) \quad (5.5)$$

which finishes the second proof of Theorem 1.

6 Proof of Theorem 2

The proof is based on the graphical construction of the Moran model; see Figure 2. We have to take into account all three different kinds of arrows. Let $R_{12} = R_{12}(t)$ be the random distance of two individuals taken at random from the Moran model at time t . In addition, $Z_3 = Z_3(t)$ and $Z_4 = Z_4(t)$ are the types of two additionally sampled individuals. We claim that in case (i)

$$\begin{aligned} \frac{d}{dt} \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] &= -\lambda \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] + 1 - \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] \\ &\quad + \alpha|\beta| \cdot \mathbf{E}_{N,\alpha}[1_{Z_3=A}(e^{-\lambda R_{23}} - e^{-\lambda R_{12}})] \\ &\quad + \alpha|\gamma| \cdot \mathbf{E}_{N,\alpha}[1_{Z_3=B}1_{Z_4=A}(e^{-\lambda R_{23}} - e^{-\lambda R_{12}})] + \mathcal{O}(1/N). \end{aligned} \quad (6.1)$$

Here, the first term describes the increase of the genealogical distance of individuals 1 and 2 if no events occur. Second, T1-arrows between 1 and 2 lead to $R_{12} = 0$ (hence $e^{-\lambda R_{12}} = 1$) at rate 1. Third, the origin of T2-arrows is with high probability $(1 - \mathcal{O}(1/N))$ neither individual 1 nor 2, but a third individual, with type Z_3 . However, this arrow only takes effect if $Z_3 = A$. Last, T3-arrows again originate from a third individual with type Z_3 . It picks a fourth individual with type Z_4 and if $Z_3 = B$ and $Z_4 = A$, the arrow takes effect. All terms require that the two/three/four chosen individuals are distinct; hence the error term $\mathcal{O}(1/N)$.

Our goal is to approximate the right hand side of (6.1). We note that the ASG implies that for all expectations on the right hand side we have that $\mathbf{E}_{N,\alpha}[\cdot] = \mathbf{E}_{N,0}[\cdot] + \mathcal{O}(\alpha)$ for small α and large N . Hence, we can use $\mathbf{E}_{N,0}[\cdot]$ as an approximation which is valid up to order α .

Recall that the mutation rate from A to B is $\theta_B/2$ and from B to A is $\theta_A/2$, as well as $\bar{\theta} := \theta_A + \theta_B$. We note that for $N \rightarrow \infty$, we can use Kingman's coalescent, since it is known to give genealogies in the large population limit of the neutral Moran model. We write $\mathbf{E}[\cdot]$ for the expectation when using Kingman's coalescent and finally argue that $\mathbf{E}_{N,0}[\cdot] = \mathbf{E}[\cdot] + \mathcal{O}(1/N)$. We obtain

$$\begin{aligned}\mathbf{E}[1_{Z_1=B}1_{Z_2=A}] &= \frac{\theta_B/2}{1+\bar{\theta}} \cdot \frac{\theta_A}{\bar{\theta}} + \frac{\theta_A/2}{1+\bar{\theta}} \cdot \frac{\theta_B}{\bar{\theta}} = \frac{\theta_A\theta_B}{\bar{\theta}} \frac{1}{1+\bar{\theta}}, \\ \mathbf{E}[1_{Z_1=A}e^{-\lambda R_{12}}] &= \mathbf{E}[1_{Z_3=A}e^{-\lambda R_{12}}] = \frac{\theta_A}{\bar{\theta}} \frac{1}{1+\lambda}, \\ \mathbf{E}[1_{Z_1=B}e^{-\lambda R_{12}}] &= \mathbf{E}[1_{Z_3=B}e^{-\lambda R_{12}}] = \frac{\theta_B}{\bar{\theta}} \frac{1}{1+\lambda}.\end{aligned}$$

Here, the first equality holds since $Z_1 = B$ and $Z_2 = A$ if and only if the first mutation event occurs before the two sampled lines coalesce. This mutation event must either be $B \rightarrow A$ in individual 1 or $B \rightarrow A$ in individual 2. Using similar arguments, we obtain

$$\begin{aligned}\mathbf{E}[1_{Z_1=A}1_{Z_2=B}e^{-\lambda R_{12}}] &= \int_0^\infty (1+\bar{\theta})e^{-(1+\bar{\theta})t} \cdot \left(\frac{1+\theta_A/2+\theta_B/2}{1+\bar{\theta}} \cdot 0 \right. \\ &\quad \left. + \frac{\theta_A/2}{1+\bar{\theta}} \mathbf{E}[1_{Z_2=B}e^{-\lambda(t+R_{12})}] + \frac{\theta_B/2}{1+\bar{\theta}} \mathbf{E}[1_{Z_1=A}e^{-\lambda(t+R_{12})}] \right) dt \\ &= \frac{\theta_A\theta_B}{\bar{\theta}} \frac{1}{(1+\bar{\theta}+\lambda)(1+\lambda)}, \\ \mathbf{E}[1_{Z_2=B}1_{Z_3=A}e^{-\lambda R_{12}}] &= \int_0^\infty (3+\bar{\theta})e^{-(3+\bar{\theta})t} \\ &\quad \cdot \left(\frac{1}{3+\bar{\theta}} \mathbf{E}[1_{Z_1=A}1_{Z_2=B}e^{-\lambda(t+R_{12})}] + \frac{1}{3+\bar{\theta}} \mathbf{E}[1_{Z_2=A}1_{Z_3=B}e^{-\lambda t}] \right. \\ &\quad \left. + \frac{\theta_A/2}{3+\bar{\theta}} \mathbf{E}[1_{Z_1=B}e^{-\lambda(t+R_{12})}] + \frac{\theta_B/2}{3+\bar{\theta}} \mathbf{E}[1_{Z_3=A}e^{-\lambda(t+R_{12})}] \right) dt \\ &= \frac{\theta_A\theta_B}{\bar{\theta}} \frac{1}{3+\bar{\theta}+\lambda} \left(\frac{1}{(1+\bar{\theta}+\lambda)(1+\lambda)} + \frac{1}{1+\bar{\theta}} + \frac{1}{1+\lambda} \right) \\ &= \frac{\theta_A\theta_B}{\bar{\theta}} \left(\frac{2+\bar{\theta}+\lambda}{3+\bar{\theta}+\lambda} \frac{1}{(1+\bar{\theta}+\lambda)(1+\lambda)} + \frac{1}{(3+\bar{\theta}+\lambda)(\bar{\theta}+1)} \right), \\ \mathbf{E}[1_{Z_2=A}1_{Z_3=B}e^{-\lambda R_{12}}] &= \mathbf{E}[1_{Z_2=B}1_{Z_3=A}e^{-\lambda R_{12}}],\end{aligned}$$

$$\begin{aligned}
\mathbf{E}[1_{Z_3=B}1_{Z_4=A}e^{-\lambda R_{12}}] &= \int_0^\infty (6+\bar{\theta})e^{-(6+\bar{\theta})t} \\
&\quad \cdot \left(\frac{1}{6+\bar{\theta}} \mathbf{E}[1_{Z_3=B}1_{Z_4=A}e^{-\lambda t}] + \frac{4}{6+\bar{\theta}} \mathbf{E}[1_{Z_2=A}1_{Z_3=B}e^{-\lambda(t+R_{12})}] \right. \\
&\quad \left. + \frac{\theta_A/2}{6+\bar{\theta}} \mathbf{E}[1_{Z_3=B}e^{-\lambda(t+R_{12})}] + \frac{\theta_B/2}{6+\bar{\theta}} \mathbf{E}[1_{Z_3=A}e^{-\lambda(t+R_{12})}] \right) dt \\
&= \frac{\theta_A\theta_B}{\bar{\theta}} \frac{1}{6+\bar{\theta}+\lambda} \left(\frac{1}{1+\bar{\theta}} + \frac{2+\bar{\theta}+\lambda}{3+\bar{\theta}+\lambda} \frac{4}{(1+\bar{\theta}+\lambda)(1+\lambda)} \right. \\
&\quad \left. + \frac{4}{(3+\bar{\theta}+\lambda)(1+\bar{\theta})} + \frac{1}{1+\lambda} \right) \\
&= \frac{\theta_A\theta_B}{\bar{\theta}} \left(\frac{7+\bar{\theta}+\lambda}{6+\bar{\theta}+\lambda} \frac{1}{(3+\bar{\theta}+\lambda)(1+\bar{\theta})} \right. \\
&\quad \left. + \frac{2+\bar{\theta}+\lambda}{3+\bar{\theta}+\lambda} \frac{5+\bar{\theta}+\lambda}{6+\bar{\theta}+\lambda} \frac{1}{(1+\bar{\theta}+\lambda)(1+\lambda)} \right. \\
&\quad \left. + \frac{1}{(6+\bar{\theta}+\lambda)(3+\bar{\theta}+\lambda)(1+\lambda)} \right)
\end{aligned}$$

Plugging the last two terms in (6.1) we find that in equilibrium

$$\begin{aligned}
\mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] &= \frac{1}{1+\lambda} + \frac{\alpha|\gamma|}{1+\lambda} \mathbf{E}_{N,0}[1_{Z_2=A}1_{Z_3=B}e^{-\lambda R_{12}} - 1_{Z_3=A}1_{Z_4=B}e^{-\lambda R_{12}}] + \mathcal{O}(\alpha^2) \\
&= \frac{1}{1+\lambda} + \frac{\alpha|\gamma|}{1+\lambda} \frac{\theta_A\theta_B}{\bar{\theta}} \frac{1}{6+\bar{\theta}+\lambda} \left(\frac{2+\bar{\theta}+\lambda}{3+\bar{\theta}+\lambda} \frac{1}{(1+\bar{\theta}+\lambda)(1+\lambda)} \right. \\
&\quad \left. - \frac{1}{(3+\bar{\theta}+\lambda)(1+\bar{\theta})} - \frac{1}{(3+\bar{\theta}+\lambda)(1+\lambda)} \right) + \mathcal{O}(\alpha^2) \\
&= \frac{1}{1+\lambda} + \frac{\alpha|\gamma|}{1+\lambda} \frac{\theta_A\theta_B}{\bar{\theta}} \frac{1}{6+\bar{\theta}+\lambda} \frac{2+\bar{\theta}+\lambda}{3+\bar{\theta}+\lambda} \left(\frac{1}{(1+\bar{\theta}+\lambda)(1+\lambda)} \right. \\
&\quad \left. - \frac{1}{(1+\bar{\theta})(1+\lambda)} \right) + \mathcal{O}(\alpha^2) \\
&= \frac{1}{1+\lambda} - \alpha|\gamma| \frac{\theta_A\theta_B}{\bar{\theta}} \frac{(2+\bar{\theta}+\lambda)\lambda}{(6+\bar{\theta}+\lambda)(3+\bar{\theta}+\lambda)(1+\bar{\theta}+\lambda)(1+\bar{\theta})(1+\lambda)^2} + \mathcal{O}(\alpha^2).
\end{aligned}$$

In particular, using a derivative according to λ at $\lambda = 0$,

$$\mathbf{E}_{N,\alpha}[R_{12}] = -\frac{\partial}{\partial \lambda} \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] \Big|_{\lambda=0} = 1 + \alpha|\gamma| \frac{\theta_A\theta_B}{\bar{\theta}} \frac{2+\bar{\theta}}{(6+\bar{\theta})(3+\bar{\theta})(1+\bar{\theta})^2} + \mathcal{O}(\alpha^2)$$

In case (ii), (6.1) changes to

$$\begin{aligned}
\frac{d}{dt} \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] &= -\lambda \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] + 1 - \mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] + \alpha|\beta| \mathbf{E}_{N,\alpha}[1_{Z_3=B}(e^{-\lambda R_{12}} - e^{-\lambda R_{23}})] \\
&\quad + \alpha|\gamma| \mathbf{E}_{N,\alpha}[1_{Z_3=A}1_{Z_4=A}(e^{-\lambda R_{23}} - e^{-\lambda R_{12}})] + \mathcal{O}(1/N).
\end{aligned}$$

As above, the term behind $\alpha|\beta|$ vanishes. Moreover,

$$\begin{aligned}
\mathbf{E}_{N,\alpha}[1_{Z_2=A}1_{Z_3=A}e^{-\lambda R_{12}}] &= \mathbf{E}_{N,\alpha}[1_{Z_2=A}e^{-\lambda R_{12}}] - \mathbf{E}_{N,\alpha}[1_{Z_2=A}1_{Z_3=B}e^{-\lambda R_{12}}], \\
\mathbf{E}_{N,\alpha}[1_{Z_3=A}1_{Z_4=A}e^{-\lambda R_{12}}] &= \mathbf{E}_{N,\alpha}[1_{Z_4=A}e^{-\lambda R_{12}}] - \mathbf{E}_{N,\alpha}[1_{Z_3=B}1_{Z_4=A}e^{-\lambda R_{12}}].
\end{aligned}$$

Therefore, in equilibrium,

$$\begin{aligned}
\mathbf{E}_{N,\alpha}[e^{-\lambda R_{12}}] &= \frac{1}{1+\lambda} + \frac{\alpha|\gamma|}{1+\lambda} \mathbf{E}_{N,0}[1_{Z_2=A}1_{Z_3=A}e^{-\lambda R_{12}} - 1_{Z_3=A}1_{Z_4=A}e^{-\lambda R_{12}}] + \mathcal{O}(\alpha^2, 1/N) \\
&= \frac{1}{1+\lambda} - \frac{\alpha|\gamma|}{1+\lambda} \mathbf{E}_{N,0}[1_{Z_2=A}1_{Z_3=B}e^{-\lambda R_{12}} - 1_{Z_3=A}1_{Z_4=B}e^{-\lambda R_{12}}] + \mathcal{O}(\alpha^2, 1/N).
\end{aligned}$$

Using the result from case (i), we are done with case (ii). Cases (iii) and (iv) are similar, because the term behind $\alpha|\beta|$ vanishes. This finishes the proof.

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